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Ashes still smoking: the influence of fire and land cover on Pantanal ecoregion amphibians

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Abstract. Fire and land cover are two elements intertwined with the natural history of organisms from seasonally dry environments. Here, we investigated the influence of fire attributes (burned area and frequently-burned area) and land cover on the relative abundance of three amphibians from the Pantanal ecoregion that belong to distinct ecomorphological groups: *Chiasmocleis albopunctata*, *Pseudis platensis*, and *Scinax acuminatus*. We systematically reviewed amphibian ecology studies in the Pantanal and analysed quantitative data between 2000 and 2021, comprising 34 sites from 12 amphibian surveys. Amphibian abundance, land cover, and fire data were assessed within buffers of a 1000 m radius. Species abundance was correlated with burned area and wetland cover. While the abundance of *C. albopunctata* and *P. platensis* decreased with burned area in the last three years, the abundance of *S. acuminatus* increased with wetland cover. Despite the claimed resilience of species inhabiting grasslands and savannas, there was substantial evidence for the influence of burned areas, even under modest human land use. Our findings illustrate that a broad array of land cover and fire attributes may influence amphibian persistence in the Pantanal ecoregion, with the magnitude depending on species traits often overlooked in modelling approaches.

Keywords: fire frequency, floodplain, natural history, wetland, wildfire.

Introduction

In the last decade, human-sparked wildfires have captured the public's attention owing to their massive impact on the environment, human health, and economy (Wang et al., 2020; Tomas et al., 2021). Fire has been intertwined with the natural history of many organisms in grasslands, savannas, and forests from seasonally dry environments. Compelling evidence shows that many communities exhibit synergies with naturally occurring fire, and some species even actively spread fire (e.g., Pivello et al., 2021). However, land conversion and ongoing climate change are reshaping ecosystems and amplifying the consequences of human-altered fire regimes (Hofmann et al., 2021; Barbosa et al., 2022).

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Fire management these days is highly context-dependent on local and regional factors, with natural fire regimes affected mainly by fire suppression and increased fire frequency (Pivello et al., 2021; Hantson et al., 2022). In seasonally dry climates, lightning-induced fires are often followed by rainfall events and occur in the dry-rainy season transition (Ramos-Neto and Pivello, 2000). On the other hand, human-induced ignitions can occur during any period, resulting in more extreme fires depending on vegetation type and weather conditions – e.g., low relative humidity/gusty winds (Hantson et al., 2022). Non-intentional fires can arise in several ways, for example, by sparked power lines and discarded cigarettes. However, burning for pasture clearing is the most common practice in many areas of central Brazil (Junk and Nunes da Cunha, 2012; Barbosa et al., 2022), which increases the chance of ignitions in areas not targeted.

The 2020 Pantanal wildfires caused the death of more than 17 million vertebrates in the ecoregion (Tomas et al., 2021). In fire-influenced ecosystems, fires may not be grievous to fauna because small vertebrates often seek refuge in holes in the ground and termite mounds or move to unburned shrubs and trees close to water (Pivello et al., 2021). However, superficial fire may evolve into a smouldering ground fire in wetland environments if the organic soil of wetlands is sufficiently dry to burn during periods of extreme drought (Watts and Kobziar, 2013; Marengo et al., 2021). Ground fire can transfer more heat to the surrounding environment (soils and plants) and often last longer. So, it may result in extensive burning with little indication of the extent (Pivello et al., 2021). Non-native invasive grasses represent an additional factor in the fire scenario for the Pantanal ecoregion, as in other Brazilian open environments. The substitution of native vegetation for African grasses increases fire occurrence and frequency, affecting the local and regional biodiversity (Rossi et al., 2014; Fusco et al., 2019). Still, studies on fire frequency and ground fires are rare in Brazil.

In particular for amphibians, information about fire effects on Neotropical species is meagre, and reviews show no clear consensus about responses to fire (Pilliod et al., 2003; dos Anjos, Solé and Benchimol, 2021). In short, the fire impacts might be either negative (Giaretta et al., 1999; Rocha et al., 2008), positive (Fredericksen and Fredericksen, 2002; Drummond, Moura and Pires, 2018), or neutral (Cano and Leynaud, 2009). Dispersal limitations, desiccation proneness, and habitat requirements can mediate amphibian sensitivity to human-landscape changes (Lion, Garda and Fonseca, 2014; Watling and Braga, 2015). Literature shows that high-intensity and frequent fires (i.e., fire intervals <2 years) compromise woody plant regeneration (Kennard et al., 2002; Balch et al., 2013). So, because of the multiple habitat requirements, fire frequency poses a severe threat to amphibian populations through an induced change in vegetation (besides direct mortality through the effects of heat and gases). However, the implications of reproductive biology and life history on the species' persistence in fire-prone landscapes are unknown. For example, leaf litter-dwelling and scansorial (i.e., species in which individuals climbed up off the ground onto vegetation) amphibians might be more vulnerable to fire than semi-aquatic ones (Batista et al., 2023). Add to the fact that the Pantanal is a cultural landscape in which current vegetation in large areas results from the management of livestock ranchers (Junk and Nunes da Cunha, 2012). While extensive livestock rearing seems more compatible with amphibian conservation than short-term crops, ground-dwelling species with aquatic reproduction seem sensitive to land cover changes (Trimble and van Aarde, 2014; Moreira et al., 2021).

Compared to surrounding Cerrado areas, amphibian assemblages from the Pantanal floodplain present a lower richness and higher abundances (Strüssmann et al., 2011). Current assessments indicated around 70 amphibian species (Neves et al., 2020), and local assemblages show the predominance of habitat-generalist species (e.g., Pansonato, Mott and Strüssmann, 2011). These species may exhibit distinct ecomorphological traits (Prado, Uetanabaro and Haddad, 2005) that should affect their relationship with fire and land cover. Here, we investigated the relationship between fire attributes and land cover on the abundance of three amphibian species. The target species are widely distributed in the Pantanal ecoregion and belong to distinct ecomorphological groups: semi-fossorial (*Chiasmocleis albopunctata* (Boettger, 1885)), semi-aquatic (*Pseudis platensis* Gallardo, 1961), and scansorial (*Scinax acuminatus* (Cope, 1862)). First, we systematically reviewed published studies on amphibian community ecology from the Pantanal. Then, we assessed the influence of land cover, burned area (BA), and frequently-burned area (FBA) on the relative abundance of the three species. Assuming that semi-fossorial frogs use underground holes for shelter more often than other groups, we would expect a harmful effect of the burned area only on scansorial species. In areas subject to frequent fires, we posit that fire would have cumulative harmful effects on amphibian abundance, even on semi-fossorial frogs, due to factors such as fire-induced habitat changes on moisture gradients (Balch et al., 2013; Watling and Braga, 2015). In addition, we expect that habitat split and fragmentation associated with human land use would strongly affect semi-aquatic frogs (Ramalho et al., 2022).

Materials and methods

Target species

All three target species have a wide distribution in open formations of central South America, including ecoregions of Cerrado, Humid and Dry Chaco, and Pantanal. *Chiasmocleis albopunctata* and *Scinax acuminatus* are explosive breeders that inhabit wetlands in savannas with low vegetation (Brasileiro et al., 2005; Prado, Uetanabaro and Haddad, 2005). The former is known to use termite mounds as shelter, whereas the latter is primarily active in low vegetation or on the ground, sheltering on terrestrial bromeliads and abandoned crab/mammal burrows (Duré and Schaefer, 2011; Duleba and Ferreira, 2014; Simioni et al., 2014). *Pseudis platensis* is a prolonged breeder associated with ponds and flooded areas (Duré and Kehr, 2001; Prado, Uetanabaro and Haddad, 2005). Although *Pseudis* spp. are associated with aquatic vegetation, terrestrial migrations are common (Strüssmann C., pers. observ.; Zank et al., 2010; Gonçalves et al., 2023).

Abundance data

We conducted a literature review on 31 January 2022, applying the PRISMA methodology (O'Dea et al., 2021). We used Clarivate Web of Science (© Clarivate, 2022) and Scopus (© Elsevier) databases to access studies on anuran species in the Pantanal. Specifically, we included the following keywords in English and Portuguese: 'amphibia' and 'Pantanal'; 'amphibians' and 'Pantanal'; 'Anura' and 'Pantanal'; 'anurans' and 'Pantanal'. Our search yielded 174 records (fig. 1). After that, we screened their abstracts and full text in some cases using three criteria: (1) focused on quantitative data rather than qualitative observations; (2) published between 2000 and 2021; (3) performed in the Brazilian portion of the Pantanal ecoregion. We restrained our search to Brazilian territory because of the availability of land cover and fire occurrence data. Fire data were available from 1985 to 2021 (see below "Land cover and fire data"). We focussed on studies conducted after 2000 to assess at least 15 years of fire legacy. We also checked additional searches fitting the screening criteria to complete our database (book chapters, unpublished field inventories, and Google Scholar).

The initial screening yielded 22 studies on amphibian assemblages in the Pantanal ecoregion (supplementary table S1). Then, we assessed these 22 surveys in more detail to minimize biases related to the sampling effort. We retained only 12 studies using pitfall trap sampling (supplementary table S1). Still, studies differed in some aspects: distance among pitfall plots, sampling effort, and combination with the active search around pitfall plots. We asked the authors for a list of pitfall coordinates when the study (including supplementary material) lacked it. So, we created a pooled abundance (i.e., all individuals of a species found in a given site) by combining data within a 1000 m circular buffer around a focal sampling plot for each of the 12 studies. Our final database comprised 34 observations at least 1.5 km apart (fig. 2).

Land cover and fire data

We extracted land cover data using QGIS (ver. 3.16) within the same 1000 m buffers used for amphibians. We used a classification produced within the scope of the MapBiomas initiative collection 7.0 (Project MapBiomas, 2022) for the precise year of each amphibian sampling. We grouped human land uses (pasture fields, crops, and pasture/crop

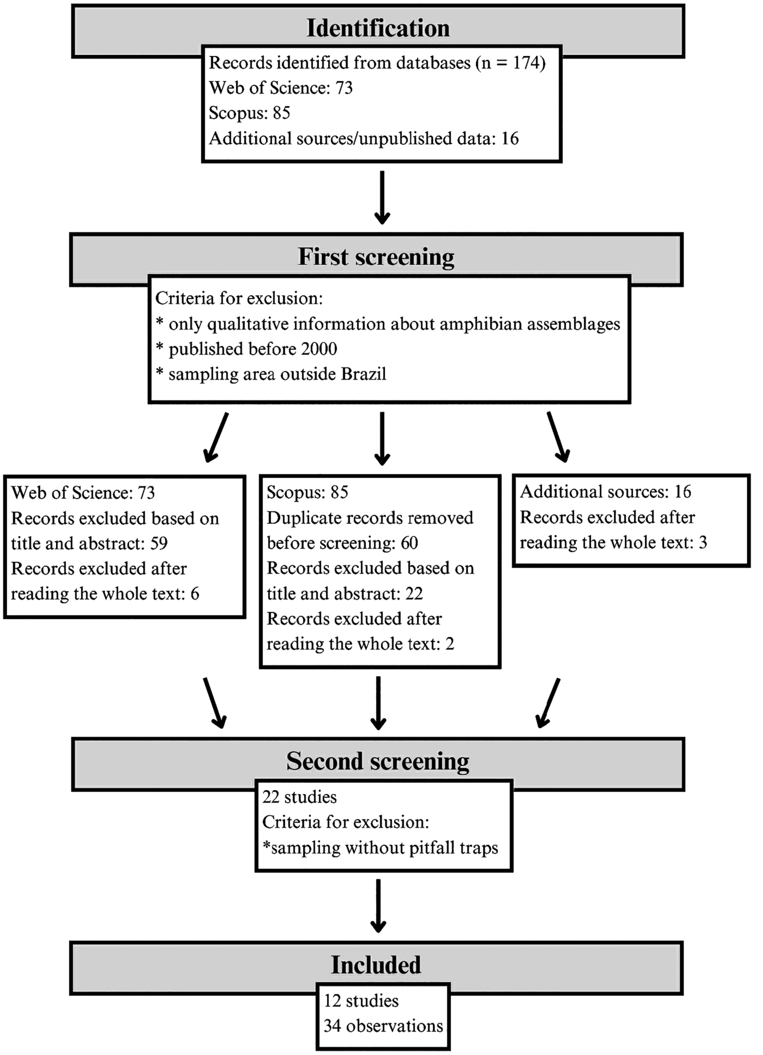

Figure 1. PRISMA diagram showing the steps of the systematic literature review on anuran species composition in the Pantanal.

mosaics) into one class. Thus, the final land cover data corresponded to five classes (forest, savanna, grassland, wetland, and land use). Data about the cumulative burned area and fire frequency were obtained in the Mapbiomas Fire platform (Project MapBiomas, 2021) using the same circular buffers. Data on fire are available in annual and monthly statistics, including frequency, between 1985 and 2021. The cumulative burned area corresponded to the increment of the burned area each year, considering pixels of 30 m × 30 m. The pixel was only counted as a fire event once, regardless of whether there was more than one fire occurrence (Project MapBiomas, 2021). The fire frequency was built by grouping the burned area each year on a single map with different classes for 1985 to 2021. So, class 1 represents the pixels that burned once, class 2 the pixels that burned two times, and so on (Project MapBiomas, 2021). To index burned area (BA), we measured the cumulative burned area in the last three years before each amphibian sampling. To index frequently-burned area (FBA), we measured burned areas in classes higher than five between 1985 and each sampling year. In practice, the fire returned at 2-3 year intervals.

Data analysis

To assess the relationship between fire attributes and land cover on the abundance of each amphibian species, we used generalized linear models (GLM). We adjusted the models for the negative binomial distribution because of residual overdispersion and asymmetry in the amphibian abundance data. The sampling effort (number of sampling days X number of traps) was included as an offset variable. Because the data set was small, we kept the candidate models simple.

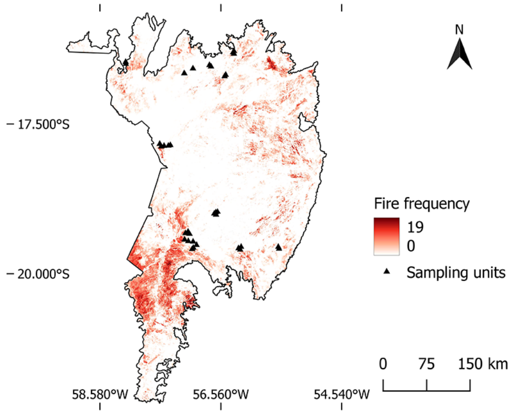

Figure 2. Location of 34 studied sites across Brazilian Pantanal, with data about fire frequency between 1985 and 2021.

We built three blocks of models assuming that fire had either no effect, effects independent of land cover, or additive to land cover. The first set included each one of the five land covers. Our second set contained only the fire attributes. We modelled BA and FBA separately because of collinearity ($r = 0.72$). Our third model set ($n = 10$) combined each land cover with fire attributes. This framework gave us a candidate set of 17 models (supplementary table S2), which we ranked using the corrected Akaike's information criteria (AIC_c).

We used multimodel inference to avoid relying on a single model to draw conclusions about the importance of variables on abundance (Mazerolle, 2006). In the top-ranked models, we used AIC_c-weighted slope estimates ± 95% confidence intervals to judge the significance of each explanatory variable. Nagelkerke pseudo-R^2 values were calculated to assess the variance explained by the top-ranked models. These analyses were performed using the packages MASS, MuMIn, and AICcmodavg (Venables and Ripley, 2002; Barton, 2020; Mazerolle, 2023) implemented in R version 4.1.1 (R Core Team, 2021).

Results

Ten of the 34 buffers showed frequently burned (FBA) patches (fig. 2). However, the FBA was modest for most buffers (<20%). Fire outbreaks were recorded in the last three years before amphibian samplings, burning around 17% of the total area (supplementary table S3). Landscape composition was variable (supplementary table S3), but human land use covered small areas. Within all investigated buffers, 1361 individuals of the target species were recorded, with *P. platensis* being the most abundant ($n = 833$). Although *C. albopunctata* ($n = 435$) and *S. acuminatus* ($n = 93$) had lower abundance, all three species were frequently recorded in the study areas (59-62%).

The model that most likely explained the abundance of *C. albopunctata* suggested that this species was influenced by BA (table 1). Three further models showed Akaike weight greater than 0.1. All the models with a weight greater than 0.1 included additive effects of BA and non-forest formations (supplementary table S2). The 95% confidence interval for the model-averaged regression excluded 0 (−3.32, −0.44) and indicated that BA within 1000 m has a negative effect on *C. albopunctata* abundance.

The relative abundance of *P. platensis* was best explained by using BA data, followed by additive effects of BA and wetland ($\Delta AIC_c = 1.24$), and BA and forest cover (table 2). There was substantial evidence for a negative effect of burned area on frog abundance, as indicated by the 95% confidence interval for BA. However, the wide interval indicated imprecise estimates (−29.9, −3.35). Forest and wetland covers did not influence *P. platensis* abundance (table 2).

For *S. acuminatus*, the best-supported models included wetland cover alone and additive effects of wetland and fire attributes (table 3). Relative abundance was higher at buffers with more wetlands within 1000 m. The narrow 95% confidence interval (0.39, 1.42) for wetland cover indicated a relatively precise estimate. Although BA and FBA were included in the best-ranked models, the 95% confidence interval for both variables included 0 (table 3).

Discussion

Our study illustrates that an interplay of land cover type and fire regimes may influence amphibian persistence in the Pantanal ecoregion, with the magnitude depending on species traits often overlooked in modelling approaches. Despite the lack of information on paleoclimate history, vegetation mosaics are linked to floods and occasional fires in the Pantanal (Power et al., 2016; Pivello et al., 2021). As a result of human activities and extreme climate, fire dynamics have changed over the past two decades, increasing burned areas in the region (Marengo et al., 2021; Correa et al., 2022). Such shifts require innovative approaches to understanding which amphibian species can thrive with the ongoing changes of the Pantanal.

Fire regimes shaped the evolution of some groups of plants and insects (Simon et al., 2009; Pausas and Parr, 2018). However, the influence of fire on amphibian evolution is still poorly understood. Contrary to our expectations, *C. albopunctata* seems affected in the short term by fire. From grasslands to humid forests, many species of *Chiasmocleis* usually live underground and show a specialized diet based on

Table 1. Highest-ranked generalized linear models and estimates explaining the relative abundance of *Chiasmocleis albopunctata*. BA: burned area.

	Number of parameters	ΔAIC_c*	Akaike weight	Model-averaged parameter (95% CI)
Model				
BA	3	0	0.46	
BA, Land use	4	2.14	0.16	
BA, Wetland	4	2.33	0.14	
Parameter				
BA				**−1.881 (−3.32, −0.44)**
Land use				0.41 (−0.34, 1.18)
Wetland				−0.31 (−1.08, 0.45)

Note: Pseudo-R^2 of the best-ranked models was between 0.23 and 0.24. Estimates in boldface type indicate that 0 is excluded from the 95% confidence interval.
*AIC_c of the highest ranked model was 185.53.

Table 2. Highest-ranked generalized linear models and estimates explaining the relative abundance of *Pseudis platensis*. BA: burned area.

	Number of parameters	ΔAIC_c*	Akaike weight	Model-averaged parameter (95% CI)
Model				
BA	3	0	0.48	
BA, Wetland	4	1.24	0.27	
BA, Forest	4	2.57	0.13	
Parameter				
BA				**−16.629 (−29.9, −3.35)**
Wetland				−0.503 (−1.20, 0.197)
Forest				−0.032 (−0.679, 0.614)

Note: Pseudo-R^2 of the best ranked models was between 0.45 and 0.47. Estimates in boldface type indicate that 0 is excluded from the 95% confidence interval.
*AIC_c of the highest ranked model was 212.93.

Table 3. Highest-ranked generalized linear models and estimates explaining the relative abundance of *Scinax acuminatus*. BA: burned area, FBA: frequently-burned area.

	Number of parameters	ΔAIC_c*	Akaike weight	Model-averaged parameter (95% CI)
Model				
Wetland	3	0	0.48	
Wetland, BA	4	1.13	0.57	
Wetland, FBA	4	1.62	0.21	
Parameter				
Wetland				**0.903 (0.39, 1.42)**
BA				−0.396 (−1.17, 0.36)
FBA				−0.306 (−0.99, 0.38)

Note: Pseudo-R^2 of the best ranked models was between 0.15 and 0.19. Estimates in boldface type indicate that 0 is excluded from the 95% confidence interval.
*AIC_c of the highest ranked model was 142.38.

ants and termites (Araújo et al., 2009; de Sá et al., 2019; Díaz et al., 2020). Because ants and termites are known to be very resilient to the effects of fire at multiple scales (Avitabile et al., 2015; Arruda et al., 2022), we speculate that their subterranean nests could represent food islands and safe shelter against fire for amphibian species that circumvent the colonies' defences (e.g., Rödel et al., 2013). The fossorial habits and specialized diet of *C. albopunctata* would be efficient traits for decreasing fire exposure. Even so, post-fire environments exhibit greater microclimate extremes (e.g., higher temperature, low humidity). Adults of *C. albopunctata* have to abandon subterranean shelters to reach temporary ponds during the breeding season. Eventually, adults and juveniles locate and return to suitable terrestrial habitats. Thus, post-fire landscape may impose constraints related to habitat split (i.e., human-induced disconnection between habitats used by different life-history stages of a species; Becker et al., 2007). Although desiccation resistance is often species-dependent (e.g., Watling and Braga, 2015), compelling evidence shows that critical split distances for Neotropical species are between 500-2000 m (Lion, Garda and Fonseca, 2014).

Our findings for *P. platensis* suggest that the BA may constrain even a semi-aquatic species closely associated with flooded habitats of the Chaco and Pantanal. The movement ecology of amphibians is poorly understood, but species' behavioural differences seem to play a crucial role in movement decisions (Rothermel and Semlitsch, 2002; Mazerolle and Desrochers, 2005; Pittman, Osbourn and Semlitsch, 2014). Studies have observed that many amphibian species, including *Pseudis* spp., seem to engage in dispersal during the transition from the rainy to dry season (Watling, Gerow and Donnelly, 2009; Moreira et al., 2017). While natural fires often occur at the beginning of the rainy season (from October to December), human-caused fires account for most fire scars during the year (Menezes et al., 2022). Although amphibians have shown inexpressive death counts during the 2020 wildfires in the Pantanal (Tomas et al., 2021), the authors point out that this value was underestimated. During extreme drought, wetlands and grasslands in the flood zone are more likely to burn (Correa et al., 2022). As a result, dispersal of semi-aquatic amphibians away from a drying pond through bare soil recently burned or facing a fire outbreak exposes individuals to dehydration risks.

While BA and FBA figured among the top-ranked models for *S. acuminatus*, there was substantial evidence only for an effect of wetland cover. Scansorial species hiding in flammable substrates, such as plants in the lower layers or litter, should display a lower resistance to fire than other species (Batista et al., 2023). Compared to *C. albopunctata* and *P. platensis*, the low abundance of *S. acuminatus* hints towards methodological issues. Sampling carried out by pitfalls may underestimate the abundance of arboreal frogs because individuals move also on shrub-arboreal strata. However, all three species were recorded at similar frequencies. In addition, reports on the natural history of *S. acuminatus* support its preference for open areas with low vegetation (Duré and Schaefer, 2011; Duleba and Ferreira, 2014; Bueno-Villafañe et al., 2022). The species seems to disperse frequently along the ground, sheltering in underground and terrestrial bromeliads. Evidence from the Pantanal shows that *S. acuminatus* uses crab burrows excavated in muddy sediments during the dry season and sporadic fires (Simioni et al., 2014). The close association with wetlands observed here suggests that *S. acuminatus* may seek refuge in the permanent waters or in burrows excavated by other animals in the case of temporary wetlands. We presume that the ongoing expansion of drier environments and the occurrence of ground fires might compromise *S. acuminatus* and species that use similar strategies. However, this hypothesis is largely speculative at this point.

To conclude, we showed that even widely distributed species differ markedly in their response to fire and land cover. Nevertheless, some aspects of natural history can help to understand how and which amphibian species can persist in fire-prone landscapes. Degrees of underground use by amphibian species seem a rich source for future research, even among species in the Hylidae family. Despite the claimed resilience of species inhabiting grasslands and savannas, there was substantial evidence for the influence of burned areas, even under modest human land use. Large-scale regional trends point to a hotter and drier Pantanal in the future (Marques et al., 2021), and therefore, an increase in the current ignition frequency is also expected. With that in mind, addressing knowledge gaps about the natural history of amphibian species (i.e., movement patterns, thermal and physiological constraints) is crucial to inform policy and management initiatives on wildfire effects.

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